RAY TRACHEID STRUCTURE IN SECOND GROWTH SEQUOIA WASHINGTONIANA

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(WITH FIVE FIGURES)

Ray tracheids are essentially a structural element in all woods of the Coniferae, and, as has been pointed out by several writers, the value of their presence or absence in taxonomy is without question. It has also been stated by several writers on this subject that as a wood structure they reach their highest development in their normal occurrence in the Pineae of the Abietineae, particularly in *Larix*, *Picea*, *Pseudotsuga*, and most notably in *Pinus*, attaining their greatest complication in the dentations and reticulations of the marginal ray tracheary cells of the hard pines. In the other two members of the Pineae, ray tracheids are normally found in *Tsuga*, but not in *Abies*. Although DEBARY (1) and PENHALLOW (6) both described them as characteristic of *A. balsamea*, this conclusion does not seem to be borne out by the work of THOMPSON (7) and Miss HOLDEN (4), who both state that ray tracheids are not to be found in this species. THOMPSON (7), however, reports them as occurring traumatically in *A. amabilis* and *A. concolor*.

In the Taxodineae, while they are entirely absent from *Taxodium*, they are notably present in *Sequoia*, and have been described by GOTHAN (3) for *S. washingtoniana*, and for *S. sempervirens* by Miss GORDON (2) and JONES (5).

In the Cupressineae they are found in all members of *Chamaecyparis*, more or less abundantly in *C. nootkatensis*, sparsely in *C. Lawsoniana*, and, according to THOMPSON (7), only under traumatic stimulus in *C. thyoides* and *C. plumosa*.

In the closely allied genus *Cupressus* they are much more abundant, frequently occurring as an entire ray one to three cells high. In *Thuya* they are also quite common, and in this genus are invariably marginal, with small bordered pits on their tangential walls, and slightly larger ones on their lateral end walls. In *Juniperus*

they are present very sparsely, but are readily recalled under traumatic stimulus. In this genus, according to Miss HOLDEN, ray tracheids usually occur as very irregularly walled cells, thickly pitted on the tangential walls, usually constituting a ray one cell high. According to PENHALLOW there are no ray tracheids in *Libocedrus*, but Miss HOLDEN reports them sparsely located under traumatic stimulus in wounded material from *L. decurrens*.

It is to be noted that while ray tracheid structure is an essential feature of the Coniferales, it is only constantly and normally present in the older genera. In the younger genera this structure may or may not be present, yet is invariably recalled under traumatic stimulus. This is in reality the general conclusion arrived at by THOMPSON (8) for *Abies*.

The foregoing résumé of the work already done in this subject is presented in an introduction to a description of a peculiar adaptation in ray tracheid structure noted in second growth wood tissue of *Sequoia washingtoniana* from the Sequoia National Forest in California. The sections were taken from the main trunk of the tree, which shows a phenomenally rapid growth not usually associated with *Sequoia*, attaining in 30 years a diameter of 19 inches at the point of section. Growth was kept up fairly regularly and consistently during the entire period.

The wood was very light in weight and very soft, was very easily cut with a knife, and capable of successful sectioning with no further treatment other than boiling. In texture the wood was harsh and coarse and somewhat inclined to be cross-grained. Sapwood was very prominent, comprising more than 90 per cent of the cross-sectional area. The growth rings were wide spaced, varying from 0.2 to 0.7 inches for a single season's growth. Microscopically the cell structure was large and thin-walled, with a very gradual transition from spring to summer wood.

As has already been stated, ray tracheid structure normally occurs in both of the present members of the genus *Sequoia*. In the mature wood of *S. washingtoniana*, two kinds of ray tracheids are to be found. First, the single, isolated, detached, radially elongated tracheary cell found on the upper and lower margins of primary rays, as is shown in fig. 1. The extent of the radial

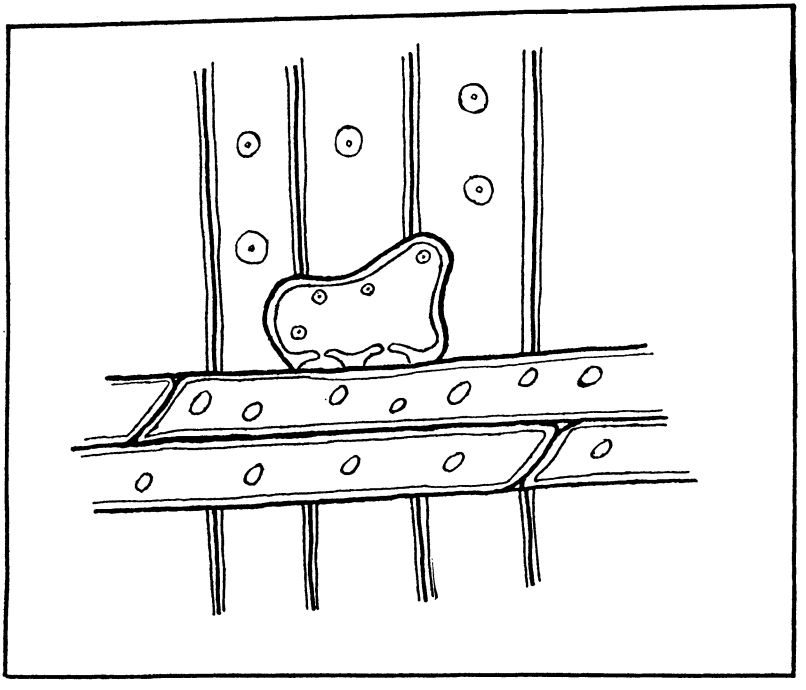

FIG. 1.—*Sequoia washingtoniana* (virgin growth): radial section showing ordinary type of isolated detached ray tracheid.

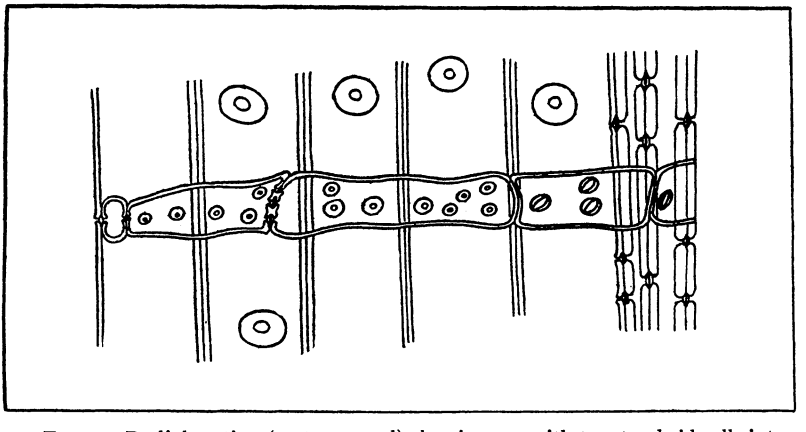

FIG. 2.—Radial section (mature wood) showing ray with two tracheid cells interspersed between ray parenchyma cells; tracheids not marginal, but components of a ray one cell high.

elongation is variable, as is also the height and the depth of the cell, which latter, however, approximates that of the ray with which it is associated. The pitting on the walls is very characteristic, especially in horizontal contact with the parenchyma cell of the ray. Second, the interspersed type of ray tracheid, as shown in fig. 2, where the tracheary cells occur in the midst of the radial prolongation of rays one cell high. They may be found singly, or in groups separated from other cells or groups of cells of similar structure by one or more parenchyma cells. Fig. 2 shows two tracheid cells occurring together with parenchymatous ray cells on either

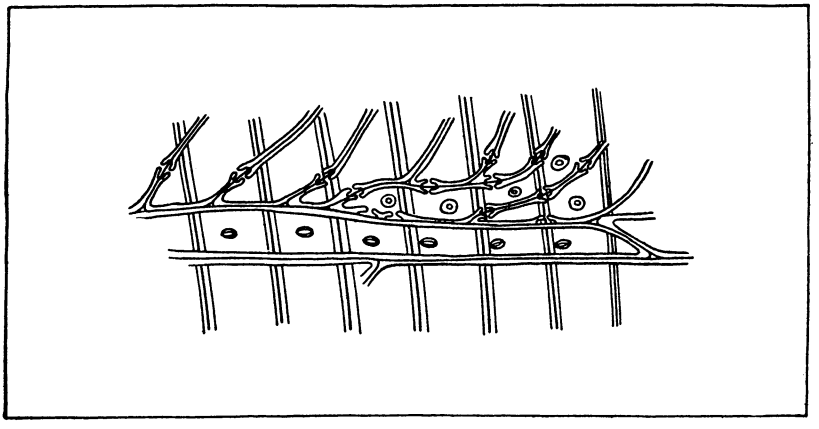

FIG. 3.—Radial section (second growth wood) showing most common form in which vertical wood tracheid is bent and prolonged along the ray to act as ray tracheid; note diversity of pitting in walls of tracheary cell.

side. In these the pitting is very characteristic, especially in the radial end walls. Miss HOLDEN has spoken of such rays as these as "secondary rays."

In contrast to the foregoing, the marginal structures on the rays of the wood of second growth *S. washingtoniana* show great variation. True ray tracheids in accordance with the previous descriptions do not occur. On the margins of the rays, however, there is a peculiar adaptation in the termination of the vertical wood tracheids directly at the ray, with the development of communicating pits in the contiguous walls of the tracheids and the

parenchyma cells of the ray. There is also evolved a radial elongation and projection of the terminating ends of the vertical tracheary elements in direction parallel to and in contact with the parenchymatous cells of the ray, with communicating pits in the intervening walls, as is shown in fig. 3. Inasmuch as true ray tracheids are not to be found, it is believed that these structures are acting as such and possess all the functions attributed to and carried on by ray tracheids.

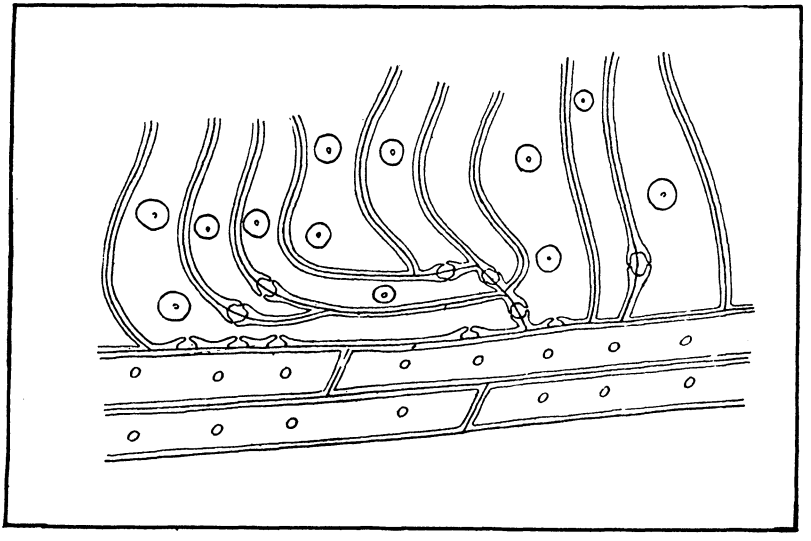

FIG. 4.—Radial section (second growth) showing wood tracheids bent and prolonged to form marginal ray tracheid two cells deep for width of two vertical wood tracheids.

It is also to be noted that in a great many cases the course of the bent-over and prolonged tracheid is imitated by those immediately contiguous with greater or less development. This is especially noticeable in fig. 4, where two neighboring and contiguous vertical tracheary elements are bent over in such a way that a ray tracheid two cells deep is evolved for the distance covered by two vertical tracheids. That these bent-over wood tracheids function as ray tracheids is evident from the double form of pitting to be found in their cell walls.

This procumbent and radial prolongation of vertical tracheary elements is to be found on either the upper or the lower margins of the rays. The direction of the prolongation may be toward the pith or toward the cambium. There seems to be absolutely no constant feature of direction which the bending shall follow, either in orientation of the one with the other or with the pith and the cambium. Along the same ray, as is seen in fig. 5, neighboring tracheids can be found bent in opposite directions and so prolonged that the end walls are in contact.

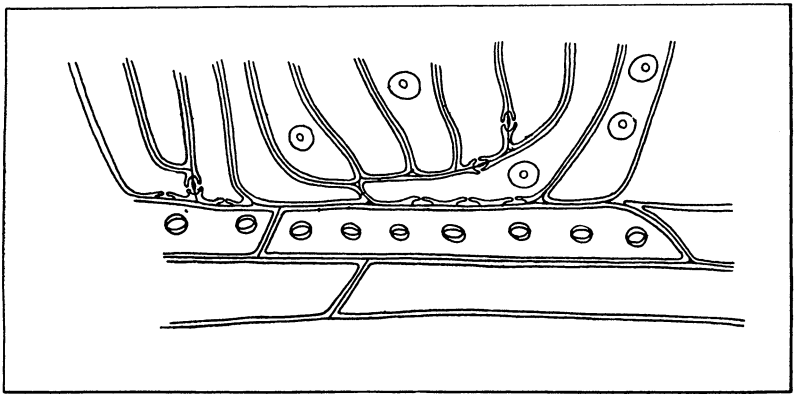

FIG. 5.—Radial section (second growth wood): adjacent wood tracheids bent in different directions along same ray.

In this second growth wood these structures were common to all parts of the stem, pith, medial sections, and cambial layers. Of the three it was perhaps least highly developed in the sections contiguous to the pith, in which there is some development of heartwood. It was found in equal frequency in either the spring or the summer wood, although, as would be expected, it was more clearly defined and capable of better figuring in the large structures of the early wood.

These structures recall and are similar to those described and figured by THOMPSON (7) in the cone axis of *Pinus Strobus*, and by JONES (5) in the mature wood of *Sequoia sempervirens*, in both of which there is ascribed similar function by the respective writers.

No attempt is made in the present article to draw any particular or general conclusions. The whole is submitted as an observation and description of a peculiar and interesting wood structure. It is to be noted, however, that these structures were found and are described in extremely rapidly grown wood tissue, and it is thought that they are special adaptations of the elements for the transference of material between the vertical and horizontal tissues, since there is an entire absence of the usual intermediary tracheary channels of communication. The origin and formation of these latter elements have been fully described and established by THOMPSON (8).

This study was undertaken at the suggestion of Professor S. J. RECORD, of the Yale School of Forestry, who also supplied a considerable portion of the material and much kindly criticism, and to whom the writer wishes to express his thanks and appreciation.

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